Common and Segregated Processing of Observed Actions in Human SPL

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To clarify the functional organization of parietal cortex involved in action observation, we scanned subjects observing 3 widely different classes of actions: Manipulation with the hands, locomotion, and climbing. An effector-based organization predicts that parietal regions involved in the observation of climbing should not differ from those involved in observing manipulation and locomotion, opposite to the prediction of an organization based upon the action performed. Compared with individual controls, the observation of climbing evoked activity in dorsal superior parietal lobule (SPL), extending into precuneus and posterior cingulate sulcus. Observation of locomotion differentially activated similar regions less strongly. Observation of manipulation activated ventro-rostral SPL, including putative human AIP (phAIP). Using interaction testing and exclusive masking to directly compare the parietal regions involved in observing the 3 action classes, relative to the controls, revealed that the rostral part of dorsal SPL was specifically involved in observing climbing and phAIP in observing manipulation. Parietal regions common to observing all 3 action classes were restricted and likely reflected higher order visual processing of body posture and 3D structure from motion. These results support a functional organization of some parietal regions involved in action observation according to the type of action in the case of climbing and manipulation.

Keywords: action observation, climbing, functional imaging, posterior parietal cortex, vision

Introduction

There is growing evidence that action observation in human and nonhuman primates involves 3 anatomical stages of processing, located in occipito-temporal cortex, corresponding to the superior temporal sulcus in the monkey, parietal cortex, and premotor cortex (Buccino et al. 2001; Jastorff et al. 2010, 2012; Nelissen et al. 2011). Thus far, such evidence relates chiefly to the grasping or manipulative hand actions generally used in action observation studies (Grafton et al. 1996; Rizzolatti et al. 1996; Decety et al. 1997; Binkofski et al. 1999; Iacoboni et al. 1999; Buccino et al. 2001; Pelphrey et al. 2005; Hamilton and Grafton 2006; Shmuelof and Zohary 2006; Gazzola et al. 2007; Peeters et al. 2009; Jastorff et al. 2010). Notable exceptions are the studies of Filimon et al. (2007) and Cross et al. (2009), in which the 3 human regions were activated by the observation of reaching actions and dancing sequences, respectively, and work by Evangeliou et al. (2009) describing the activation of monkey parietal cortex by observing reaching.

The functional organizations of the parietal and premotor levels are currently disputed. Initially, it was suggested that both cortices were somatotopically organized (Buccino et al. 2001). A subsequent study, in which the effectors and types of actions were manipulated independently, confirmed the somatotopic organization of premotor, but not parietal cortex. On the contrary, parietal cortex near the putative human AIP (phAIP) was organized according to the type of action observed: Actions in which the object was moved toward the actor activated a more anterior part of phAIP than did the opposite actions, an organization independent of the effector (Jastorff et al. 2010). This sort of organization differs from that assumed for the posterior parietal cortex (PPC) of the macaque. This region is generally described as comprising distinct areas controlling different effectors: The posterior parietal reach region controlling the arm, lateral intraparietal area (LIP) controlling area the eye, and anterior intraparietal area (AIP) controlling area the hand (Andersen and Cui 2009), although electrical stimulation experiments have suggested more functional descriptions (Cooke et al. 2003). One way to reconcile these views was to state that phAIP was involved in the observation of manipulative actions, independently of the effector used, because these were typically performed with the hand (Jastorff et al. 2010). These authors described the functional organization of only a single parietal region, phAIP, a finding that is open to 2 interpretations. The functional organization could be a characteristic of that particular area or, alternatively, such organization may be a general property of the parietal cortex. The present experiments were undertaken to distinguish between these alternatives.

To this end, we have contrasted effectors and classes of actions. The various hand actions used in (Jastorff et al. 2010) were utilized here as the class of manipulative hand actions. As a second, markedly different class of actions, we presented bipedal locomotion, involving only the feet. For the third, most critical action class, we used climbing actions involving both hands and feet. An organization according to action "class," as put forward by Jastorff et al. (2010), predicts that regions involved in observing climbing should differ from both those involved in observing manipulation and those involved in locomotion. An organization according to the "effector" predicts that regions involved in observing climbing should not differ from both those involved in observing manipulation and those involved in observing locomotion, since these actions share effectors. Each hypothesis predicts the activation of different regions by observing manipulation and observing locomotion. Thus, if we consider the observed actions pairwise, 2 pairs make opposite predictions for each type of organization: Observing manipulation and climbing and observing locomotion and climbing. The discriminative power of the latter pair may be weak, however. It could be argued that bipedal locomotion is a simplified, evolutionarily more recent, version of climbing, considered a type of quadri-

pedal locomotion, and that observing locomotion should therefore include a subset of regions involved in observing climbing. If we accept this view, then comparing the regions involved in observing locomotion and climbing is not particularly informative, and we have only a single test remaining with which to distinguish between alternative hypotheses.

Stronger predictions are possible, however, by focusing on regions more strongly activated for observing 1 class of actions compared with the other 2. Indeed, the action class hypothesis predicts separate regions for each of the 3 tests, while the effector hypothesis predicts the opposite result, since at least one of the elements of the conjunction will not hold. Thus, even if we assume that locomotion and climbing are functionally similar (see above), we are still left with 2 informative tests, rather than 1 for the pairwise testing, since the remaining 2 tests, focusing on manipulation regions and climbing regions, will distinguish between the alternative hypotheses. In the present study, we measured functional magnetic resonance imaging (fMRI) responses elicited by the observations of manipulation, climbing, and locomotion to test which of the 2 predictions was best matched by the activation pattern actually observed in the parietal cortex: Those of the functional hypothesis or those predicted by the effector hypothesis.

Materials and Methods

Subjects
Fifteen right-handed volunteers (8 females) with normal or corrected-to-normal visual acuity and no history of mental illness or neurological disease participated in the main experiment. Their age averaged 24 years (range 21–28 years). Four of them (mean age, 25 years, 3 females) and 1 additional volunteer (21 years, male) participated in the control experiments. They were paid for their participation in the experiment. The study was approved by the Ethical Committee of the KU Leuven Medical School, and all volunteers gave their written informed consent in accordance with the Helsinki Declaration before the experiment.

The stimuli were displayed using an LCD projector (Barco Reality 6400i, 1024×768 pixels, 60-Hz refresh frequency) on a translucent screen positioned in the bore of the magnet at a distance of 36 cm from the subjects' eyes. Participants viewed the stimuli through a mirror tilted at 45° and attached to the head coil. They were asked to bite an individually molded bar fixed to the scanner table to reduce head motion during the scanning sessions. They were orally instructed to fixate a target in the center of the screen, and eye positions were recorded with an ASL 5000 eye tracking system (Applied Science Laboratories, 60 Hz) throughout the session.

Stimuli and Experimental Conditions of Main Experiment
Experimental stimuli consisted of video clips (448×336 pixels, 60 Hz) showing an actor in the center of the display, viewed from the side,

performing various manipulative hand actions, locomotion, and climbing. Each action class included 16 videos, showing 4 different exemplars of a given class. The videos of manipulative hand actions featured human actors performing manipulative hand actions using their right hands. The action exemplars included pushing, placing, grasping, and dragging an object, 3 of which are similar to those of the (Jastorff et al. 2010) study. The locomotion videos showed human actors walking, running, stepping over an obstacle, or descending a stair. Finally, the action class "climbing" included the exemplars climbing up a rock face, a tree, or a ladder, or climbing over a table. A single frame taken from each of the 3 classes of actions is shown in Figure 1. All videos were recorded expressly for our purposes, except rock climbing, which was retrieved from the internet. The videos of manipulative hand actions and 3 locomotion videos (walking, running, and stepping over an obstacle) were taken indoors. The other videos were shot outdoors, and since the background was more distant, background motion was relatively slow. In the manipulative videos, the dark background, similar to that in Jastorff et al. (2010), was stationary. In the 3 locomotion videos, taken indoors, the green background was close to the subject, thus background motion was relatively fast. Therefore, the background in these videos was replaced by a gray, textured pattern that remained stationary. In the 4 climbing videos and the video of descending the stairs, the background was an integral part of the scene and could not be manipulated. As a consequence, it moved slowly at a constant speed in those videos. In each of the 3 classes, we had several male and female actors performing the actions, resulting in 10 or 11 actors for each action class.

Two types of control stimuli were used. An "action" is defined by integrating 2 main components: A figural component (shape of the body) and the motion component (motion vectors of the body). To control both, we used static images taken from the action videos, and "dynamic scrambled" stimuli derived by animating a noise pattern with the motion extracted from the original action videos. The static images consisted of 3 frames taken from the beginning, middle, and end of the video to capture the shape of the actor's body at different stages during the action. These images controlled both for the shape of the body or body part and for shapes of objects present in the scene, as well as for lower order static features such as spatial frequency. To create dynamic scrambled control videos, the local motion vector was computed for each pixel in the image on a frame-by-frame basis (Pauwels and Van Hulle 2009). Subsequently, these vectors were used to animate a random-dot texture pattern (isotropic noise image). The resulting videos contained exactly the same amount of local motion as the originals, but no static configuration information. Yet, actions such as walking and running could still be perceived because of the global motion pattern. Therefore, each frame of the video was divided into 48 squares, with the starting frame randomized for each square, thereby temporally scrambling the global motion pattern. This procedure eliminated the global perception of a moving human figure, but within each square, local motion remained identical to that in the original video. Dynamic scrambled videos had the same mean contrast and brightness as the original videos. Each video clip had its corresponding 2 types of control stimuli, resulting in a 3×3 design with factors "class of action" (3 levels) and "type of video" (3 levels). To assess the visual nature of the fMRI signals, we included an additional baseline fixation condition. In this condition, a

Figure 1. Frames taken from videos of the 3 action classes. From left to right: Manipulative hand actions (exemplar, grasping), locomotion (exemplar, walking), and climbing (exemplar, rock climbing). The actual videos were in color. The fixation point, indicated by a cross, is shown larger than in the real videos for clarity. For manipulative actions, 2 different fixation targets were used. In the locomotion videos, subject moved either to the left or to the right. In climbing, they moved also in up- and downward directions

gray rectangle of the same size and average luminance as the videos was shown. We thereby minimized luminance changes across the conditions, thus keeping the pupil size constant during the experiment.

All videos measured 17.7° by 13.2° and lasted 2.6 s. The edges of videos were blurred with an elliptical mask (14.3° × 9.6°), leaving the actor and the background of the video unchanged, but blending it gradually and smoothly into the black background at the edges. A 0.2° fixation target was shown in all conditions. For manipulative hand action videos, in which motion was very local, the target was presented above or below the position where the movement occurred in the video to control for retinal position. This target position was constant either above or below throughout one run but changed between runs. For other conditions (locomotion, climbing videos, and baseline), it was presented at the center of the videos. For control stimuli, the fixation point was at the same position as in the original videos.

Procedure of the Main Experiment
Two types of stimulus sequences or "runs" were generated: Those using static images as controls and those using dynamic scrambled videos. Thus, the initial 3 × 3 design was subdivided into two 3 × 2 designs. Each run included 6 experimental conditions and the fixation baseline condition. These 7 conditions were shown 3 times in 21-s blocks, with runs lasting 441 s. Each experimental block included 8 videos of a given class, corresponding to 4 action exemplars and both genders. Both the individual videos and the order of the blocks were selected pseudorandomly, and counterbalanced across runs and participants. Over the course of 2 runs, all the different video clips for a given class were shown 3 times. In the runs with static control conditions, each static block of a given class used a different frame of the video (start, middle, and end). Four runs of each type (8 in total) were sampled per subject during a single session. Every run started with the acquisition of 4 dummy volumes to assure that the fMRI signal had reached its steady state.

Control Experiment
In 12 of the 16 original locomotion videos, the background was replaced by a gray static textured pattern. To investigate the effect of background motion, we recorded 12 new locomotion videos outdoors, showing walking, running, and stepping over an obstacle, without changing the background. These 12 new videos, together with the 4 original exemplars showing the actor descending a stair, comprised a new condition: Locomotion with background, locomotion$_{bg}$. Control conditions were derived from this new action condition exactly as in the main experiment. In addition to these 2 new conditions, 4 conditions, corresponding to climbing actions, locomotion, and their controls, were the same in the control as in the main experiment. Hence, each run included 6 experimental conditions and the fixation baseline condition, exactly as in the main experiment. This allowed us to assess the effect of removing the background in the original locomotion videos. Two types of runs were again generated, those using static images as controls and those using dynamic scrambled videos and, as in the main experiment, 8 runs (4 with static and 4 with dynamic controls) were acquired per subject in a single session.

Scanning
fMRI data were acquired with a 3T magnetic resonance (MR) scanner (Intera, Philips Medical Systems, Best, The Netherlands) located at the University Hospital of the Catholic University Leuven. Functional images were acquired using gradient-echoplanar imaging with the following parameters: 50 horizontal slices (2.5 mm slice thickness; 0.25 mm gap), repetition time (TR) = 3 s, time of echo (TE) = 30 ms, flip angle = 90°, 80 × 80 matrix with 2.5 × 2.5 mm in plane resolution, SENSE reduction factor of 2. The 50 slices of a given volume covered the entire brain from the cerebellum to the vertex. A 3D high-resolution, T_1-weighted image covering the entire brain was acquired in one of the scanning sessions and used for anatomical reference (TE/TR 4.6/9.7 ms; inversion time 900 ms, slice thickness 1.2 mm;

256 × 256 matrix; 182 coronal slices; SENSE reduction factor 2.5). The scanning session lasted about 120 min.

Data Analysis and Statistical Processing
Image processing was carried out using SPM5 (Wellcome Department of Imaging Neuroscience, London, United Kingdom), implemented in MATLAB (The Mathworks, Inc.). Preprocessing included realignment of the images, co-registration of the mean functional image with the anatomical image, and normalization of all images to standard stereotaxic space [montreal neurological institute (MNI)] with a voxel size of $2 \times 2 \times 2$ mm^3. Normalized images were smoothed by a Gaussian kernel (full width at half maximum 8mm). The 2 types of runs were analyzed separately, with each type corresponding to a 3 × 2 design. For each subject, the duration of conditions and onsets was modeled by a General Linear Model. The design matrix was composed of 13 regressors: 7 regressors modeling each of the conditions used (3 actions, 3 controls, and 1 baseline) and 6 regressors from the realignment process (3 translations and 3 rotations). All regressors were convolved with the canonical hemodynamic response function.

Main Experiment
Six main contrasts were defined for each individual subject at the first level comparing observing the 3 classes of actions with their static and dynamic scrambled controls, respectively. In a second random-effect analysis (Holmes and Friston 1998), we computed 3 different statistical parametric maps (SPMs) by taking the conjunction (conjunction null, Nichols et al. 2005) of the 2 contrasts, defined for observing a given action class, by the 2 types of controls (action minus static and action minus dynamic scrambled). In the following account, we refer to this conjunction as the "activation map" of observing the action class. This activation map indicates the network of brain regions significantly activated by the observation of that action class. To define the activation map of each action class, we used a threshold of $P < 0.05$ FDR corrected for the conjunction. This threshold was lowered to $P < 0.01$ uncorrected for illustrative purposes. To guarantee that the SPMs corresponded to visually responsive regions, the activation map of a given class was inclusively masked by the contrast of that action class versus baseline (visual mask), thresholded at $P < 0.05$ uncorrected.

Next, we performed an interaction analysis to determine the regions that were differentially activated by the observation of a particular action class compared with the observation of the 2 remaining classes of actions. This interaction analysis ensures that the differences reported cannot be explained by lower order factors also present in the control conditions. Instead of computing 2 interactions for each action class comparison, 1 for static and 1 for dynamic scrambled controls, and then subsequently conjoining them, we generated a single interaction term, combining both controls within the same model. Thus, we defined 6 interactions by comparing the observation of each action class to that of the other 2 classes. These interaction terms were of the form [action$_x$ − (1/2 static$_x$ + 1/2 dynamic scrambled$_x$)] − [action$_y$ − (1/2 static$_y$ + 1/2 dynamic scrambled$_y$)], in which x indicates 1 of the 3 classes and y 1 of the 2 remaining classes. These 6 interactions were computed for individual subjects at the first level and subsequently subjected to random-effects analysis. The resulting SPMs were labeled "observing class x > observing class y" to indicate the direction in which the interaction was taken. The conjunction of the 2 interaction SPMs for a given class (e.g. observing manipulation > observing climbing and observing manipulation > observing locomotion) was next computed (conjunction null, Nichols et al. 2005) and thresholded at $P < 0.05$ FDR corrected. The resulting map was then inclusively masked with the activation map at 0.05 uncorrected and the visual mask at the same level (see above). The purpose of the masking with the activation map was to restrict the interactions to those arising from stronger activations in the action class under consideration rather than those of a control condition. Indeed, the interaction term is of the form (A–B)–(C–D) and can show activation either because activity in A (here the observation of the class being considered) or in D (the control for the other class) is high. The masking also ensured that the retained voxels showed

some degree of interaction for both controls, since the activation map was defined relative to both controls. These operations ensured only that one action class activated a voxel more than the other 2 classes, relative to the controls, and that this effect was visual in nature and due to the action condition rather than the controls. To guarantee that the voxel was differentially responding only to observing a single action class, we excluded all voxels from the interaction conjunction that showed stronger activation for one of the other action classes compared with either its controls. This was done exclusively by masking the interaction conjunction with the 4 contrasts, defining the activation by the other 2 classes for the 2 control conditions, at a low threshold ($P < 0.03$ uncorrected) to enhance the specificity. This later threshold was a compromise between values as low as possible to ensure maximum specificity of the interaction maps, and a threshold too low to guarantee the specificity of the regions excluded. This set of operations, including a conjunction, 2 inclusive and 4 exclusive masks, defined the "interaction maps" for each of the action classes. Given that this interaction map involved a comparison with a large number of conditions and excluded even weak responses to observation of the other action classes, the resulting voxels will be described as "specific" for observing the class.

Finally, to define the cortical regions that were activated by observing all 3 actions, or by observing pairs of them, we simply took the conjunction of all 3 or of pairs of activation maps in a random-effects analysis. These "common activation maps" were also thresholded at $P < 0.05$ FDR corrected. For illustrative purpose, the threshold was lowered to $P < 0.01$ uncorrected just as for the individual activation maps. The individual and common activation maps and the interaction maps for each class were projected (enclosing voxel projection) onto flattened left and right hemispheres of the human PALS B12 atlas (Van Essen 2005) using Caret (Van Essen et al. 2001).

Activity profiles plot the mean (and standard error), across subjects, of the %MR signal change from the fixation baseline for the different conditions of the experiment. Such profiles were computed for the local maxima or representative voxels by averaging the 27 voxels surrounding the local maxima or representative voxels, corresponding to a volume of 216 mm³. This ROI size represents the compromise between local and representative data, used in many of our previous studies. Activity profiles were also calculated for regions of interests (ROIs) defined by the activation maps in the premotor cortex. We used the miniROIs of the premotor cortex defined by Jastorff et al. (2010), to capture variations in premotor activity along a dorso-ventral direction. Given the extent of the premotor activations in the present study, we added 5 miniROIs in the left hemisphere and 8 in the right, and also slightly altered the next 3 miniROIs of the right hemisphere so as to completely cover the activations. Following Jastorff et al. (2010), we identified the voxels included in each of the miniROIs, exported them to MNI space, and removed any voxels common to 2 miniROIs. MR signals were averaged over all voxels included in the miniROI. In total, we defined 46 miniROIs over premotor cortex (right hemisphere: 25, left hemisphere: 21), including an average of 19 (±6) voxels.

Control Experiment

Given the small number of subjects ($n = 5$), a fixed-effects analysis was performed. The climbing and locomotion activation maps were defined exactly as in the main experiment by a conjunction between contrasts with the 2 control conditions. The difference between the conditions observing locomotion with or without background was assessed in 2 ways. First, the 2 versions of locomotion were directly compared by computing the SPMs for interactions in both directions between the factors "locomotion/control" and "background present/absent", averaged over the 2 types of controls. These interaction maps were thresholded at $P < 0.05$ FDR corrected, but also at a lower level of $P < 0.01$ uncorrected, to increase the sensitivity of the test. Secondly, the interactions "climbing > locomotion" were computed for the 2 versions of locomotion. Both interaction maps were thresholded at $P < 0.05$ FDR corrected and directly compared. To further explore these 2 maps, we compared in the neighborhood of the maxima obtained for the interaction climbing > locomotion in the main experiment, the local maxima in the interaction climbing > locomotion and

in the interaction climbing > locomotion$_{bg}$ obtained the control experiment. Finally, ROIs were defined by taking 27 voxels around the local maxima of the interaction climbing > locomotion from the control experiment. The local maxima located closest to the ones obtained from the main experiment were chosen. In these ROIs, the interactions between the factors "action/control" and "background present/absent" were tested with a 2 × 2 ANOVA across runs, pooled over the 5 subjects.

Results

Fixation Behavior

For technical reasons, eye position data were recorded for only 11 of the subjects participating in the main experiment. These subjects fixated well during the scanning, averaging 4.8 (range 3.8–5.9) and 4.6 (range 3.8–5.2) saccades per minute in the runs with static and dynamic scrambled control conditions, respectively. More importantly, the number of saccades did not differ significantly across the 7 conditions of these runs, as tested by 1-way ANOVAs: $F_{6,70} = 0.6$, ns and $F_{6,70} = 0.11$, ns for static and dynamic scrambled runs, respectively. In the control experiment, all 5 subjects fixated very well, averaging 2.6 (range 2.0–3.0) and 2.9 (range 2.4–3.3) saccades per minute in the static and dynamic scrambled control conditions, respectively. There was no significant difference in the number of saccades across conditions: ANOVAs $F_{6,259} = 0.2$ and $F_{6,259} = 0.17$, both ns, when each run was considered separately, as in the fixed effect model (results were very similar when the runs were averaged per subject and statistics tested across subjects).

Regions Involved in the Observation of a Given Class of Action: Action Class Activation Maps

In the first analysis of the main experiment, we investigated the cortical regions involved in observing the 3 different classes of actions. For this purpose, we compared a given action observation to each of its 2 control conditions and took the conjunction of these 2 contrasts (see Materials and Methods). Figure 2 shows the contrast between observing climbing actions and their respective static controls in red, and the contrast between observing climbing actions and their dynamic scrambled controls in green, both at $P < 0.05$ FDR-corrected level. The yellow voxels correspond to the overlap between red and green voxels, while the blue voxels correspond to the conjunction of the 2 contrasts at $P < 0.05$ FDR corrected. These latter voxels overlapped almost perfectly with the voxels common to the 2 individual contrasts. The blue voxels visualize the network of regions differentially activated by the observation of climbing actions, the activation map for observing climbing. These activation maps are shown on the folded brain and also on the flattened hemispheres. It is noteworthy that when observation of climbing is contrasted only with its dynamic scrambled control, ventral occipital and temporal regions are activated, probably reflecting activation by the scenes (Epstein and Kanwisher 1998; Hasson et al. 2003) present in the background of those videos (Fig. 1).

The regions differentially activated by the observation of climbing actions, that is, the activation map for observing climbing defined by the conjunction of contrasts with the 2 control conditions (each contrast at $P < 0.05$ FDR corrected), are plotted in Figure 3A in shades of yellow, along with the
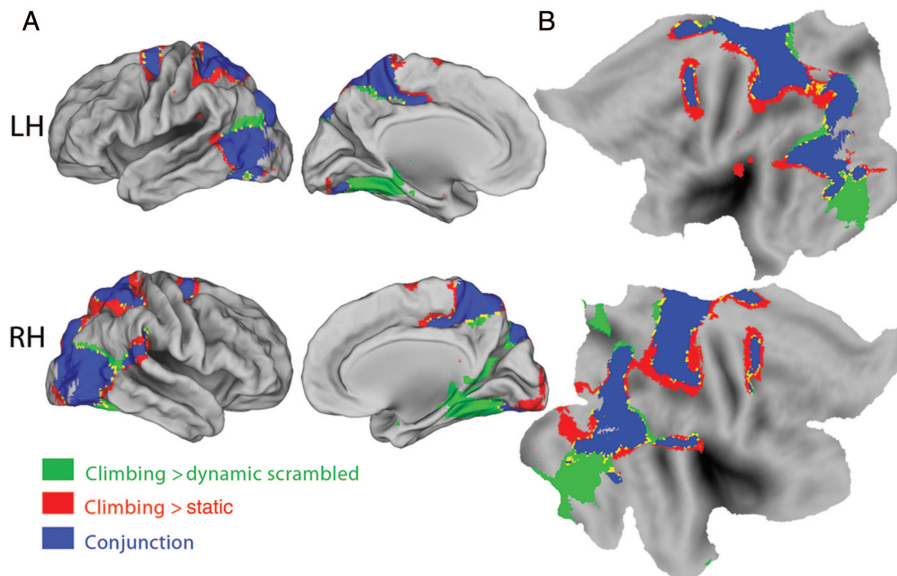
Figure 2. Definition of the activation map for the observation of climbing. SPMs plot the voxels that are significantly activated in the contrast "observation of climbing actions" versus "static control" (red), the contrast observation of climbing actions versus "dynamic scrambled control" (green), both at $P < 0.05$ FDR corrected, their overlap (yellow) and their conjunction (blue). All 3 contrasts were inclusively masked with "climbing observation" versus "fixation" ($P < 0.05$ uncorrected). These maps are shown on the lateral and medial views of the 2 hemispheres of the folded cortical surface (A) and on the flatmaps of the hemispheres (B). LH and RH: left and right hemispheres.

local maxima of the activation (red dots). The black outlines correspond to the activation map defined at lower threshold ($P < 0.01$ uncorrected, see Materials and Methods) for illustrative purposes. The distance between these outlines and the colored voxels provides an indication about the steepness of the activation pattern. The local maxima for observing climbing actions include the human motion complex (hMT/V5+) and some of the satellites of human MT/V5 (pFST and pV4t, Kolster et al. 2010), posterior fusiform, anterior and dorsal superior parietal lobule (SPL), ventral and dorsal occipital part of intraparietal sulcus (IPS), anterior and middle part of precuneus, posterior cingulate sulcus, posterior superior frontal gyrus (pSFG), and precentral sulcus, all bilaterally, and right superior temporal sulcus (STS; Table 1).

Figure 3B shows the regions involved in observing locomotion, that is, the activation map for locomotion. The overall topography of the network was similar to that for the observation of climbing actions, but activations were weaker, notably in dorsal SPL and right premotor cortex. The local maxima (green dots in Fig. 3B) include the human motion complex (hMT/V5+) bilaterally, middle temporal gyrus (MTG) bilaterally, right STS and right lateral occipital cortex, anterior SPL bilaterally, dorsal IPS medial (DIPSM) bilaterally, dorsal and ventral occipital IPS bilaterally, left posterior cingulate sulcus and left pSFG, and precentral sulcus (Table 1).

Figure 3C shows the regions involved in the observation of manipulative hand actions, that is, the activation map for manipulation. While the activation sites in occipito-temporal cortex are rather similar to those for observing climbing and locomotion, the parietal activation sites are more restricted and are located closer to the IPS. The premotor activations are limited to the more ventral sites. The local maxima (blue dots in Fig. 3C) include the human motion complex (hMT/V5+) bilaterally, STS bilaterally and right superior temporal gyrus (STG), anterior SPL bilaterally, left anterior IPS, right DIPSM, and precentral sulcus bilaterally (Table 1). The parietal

activation is more asymmetric, favoring the left hemisphere, than to the other 2 networks, in agreement with earlier observations (Jastorff et al. 2010), and likely represents the asymmetry in the manipulation videos.

Figure 4 directly compares the activation patterns for the observations of the 3 classes of actions, using the activation maps for observing the 3 classes at $P < 0.01$ uncorrected, that is, the conjunctions at a lower threshold, in order not to overestimate differences between networks. This figure, which generalizes the earlier studies by exploring a much wider range of actions, clearly shows that most of the SPL on the lateral surface of the hemisphere is activated by the observation of actions. This activation extends into the anterior part of the precuneus, considered by Brodmann to be part of the same cytoarchitectonic field (BA7). In addition, parieto-occipital cortex, particularly the posterior bank of the occipital part of the IPS, is also involved. At the premotor level, the posterior part of the superior frontal gyrus (SFG) is activated to an extent not previously reported. Finally, the occipito-temporal activation extends in 2 directions (Jastorff and Orban 2009): Into posterior MTG/STS and STG, and into the occipito-temporal sulcus/fusiform gyrus.

Figure 4 also illustrates that several regions of the action observation network are commonly activated by all classes of actions, whereas other regions seem to be activated primarily by only 1 or 2 of the classes. At the occipito-temporal level, posterior MTG, STS, and STG were activated by observing all 3 action classes. Also at the parietal level, parts of the SPL were commonly activated, and this common region extended rostrally into the dorsal part of the postcentral sulcus. However, activation for observing climbing and for observing locomotion extends far more dorsally in the SPL compared with observing manipulation and continues onto the medial wall, while activation for observing manipulation extends somewhat more ventrally into the confidence ellipse of phAIP compared with the other 2 classes. In parieto-occipital cortex,
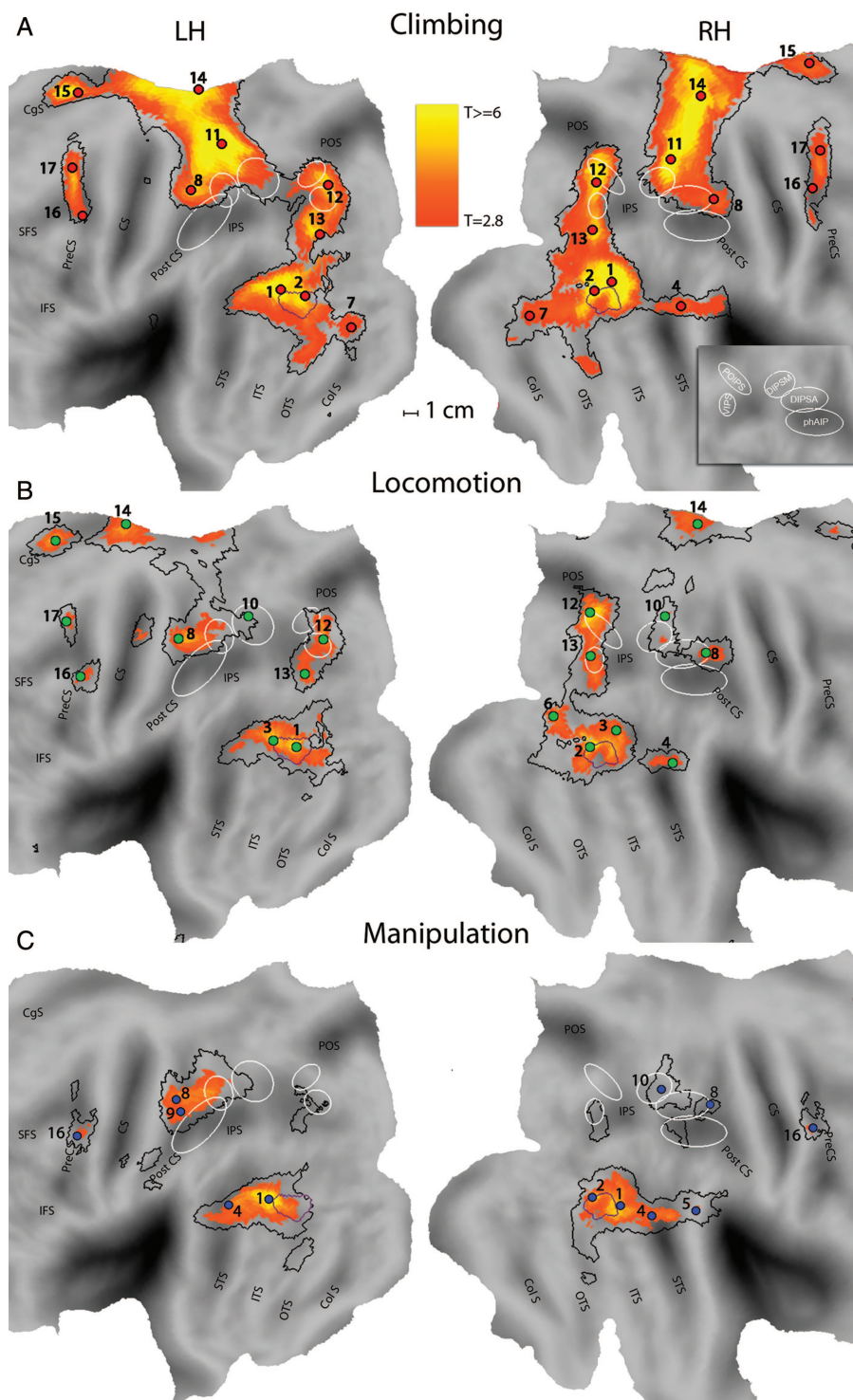
Figure 3. Activation maps for the observation of the 3 classes of actions. SPM showing the voxels significant (orange to yellow) in the conjunction of the contrasts observation of climbing (*A*), locomotion (*B*), or manipulation (*C*) versus static and dynamic scrambled controls, inclusively masked with the contrast observation of climbing (*A*), locomotion (*B*), or manipulation (*C*) versus fixation (*P* < 0.05 uncorrected), projected onto the flatmaps of the left and right hemispheres. Color scales indicate the *t*-scores for the conjunction, *t*-values of 2.87 (*A*), 3.22 (*B*), and 3.34 (*C*) corresponding to *P* < 0.05 FDR corrected. The black outlines include all voxels reaching *t* = 2.3, corresponding to *P* < 0.01 uncorrected, shown for illustrative purposes. Spatial scale is indicated. Red (*A*), green (*B*), and blue (*C*) dots: local maxima of the conjunctions, as numbered in Table 1; white ellipses: From front to back confidence limits for putative human AIP (phAIP), dorsal interparietal sulcus anterior (DIPSA), and medial (DIPSM) regions, all 3 taken from Jastorff et al. (2010), parieto-occipital intraparietal sulcus (POIPS) and ventral intraparietal sulcus (VIPS) regions (see insert); purple outline: hMT/V5+ taken from Jastorff and Orban (2009). CgS: cingulate sulcus, SFS: superior frontal sulcus, IFS: inferior frontal sulcus, PreCS: precentral sulcus, CS: central sulcus, PostCS: postcentral sulcus, IPS: intraparietal sulcus, POS: parieto-occipital sulcus, STS: superior temporal sulcus, ITS: inferior temporal sulcus, OTS: occipito-temporal sulcus, ColS: collateral sulcus.

Table 1

Local maxima for observation of the 3 classes of actions

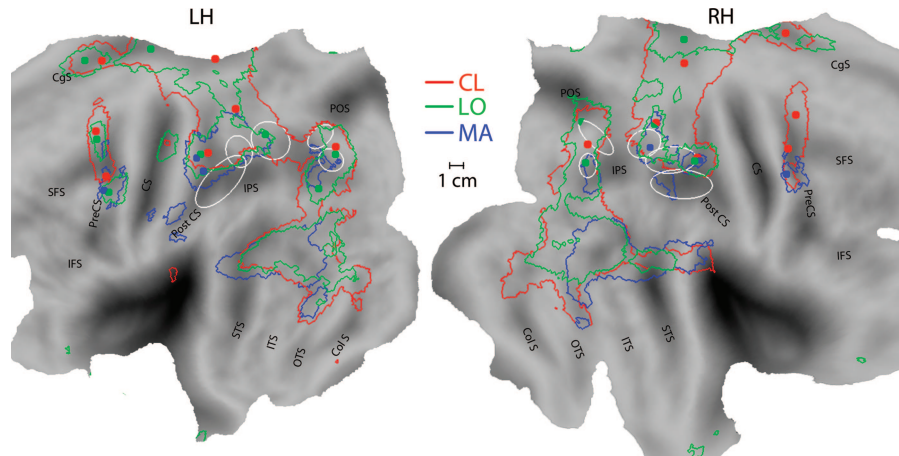| Location		Manipulation		Locomotion		Climbing	
		LH	RH	LH	RH	LH	RH
Occipito-temporal							
1	hMT/V5+	−50, −68, 6	54, −68, 6	−48, −70, 6		−48, −72, 6	50, −70, 6
2	MT/V5 satellites		48, −76, −2		46, −76, −2	36, −78, −6	46, −76, −2
3	MTG			−38, −64, 6	42, −68, 14		
4	STS	−52, −54, 10	54, −46, 10		58, −44, 14		58, −42, 16
5	STG		66, −36, 24				
6	Lateral occipital (V4/V3v)				28, −88, −4		
7	Posterior fusiform					−26, −88, −6	26, −76, −6
Parietal							
8	Anterior SPL	−34, −38, 62	32, −40, 58	−30, −36, 60	32, −40, 58	−30, −40, 58	34, −40, 58
9	Anterior IPS	−42, −38, 58					
10	DIPSM		26, −56, 60	−24, −60, 58	22, −56, 62		
11	Dorsal SPL					−16, −56, 64	22, −58, 64
12	Dorsal occipital IPS			−22, −86, 38	20, −78, 34	−20, −82, 48	22, −82, 40
13	TOS/occipital IPS			−30, −86, 26	28, −78, 26	−30, −88, 20	32, −80, 20
14	Anterior precuneus			−10, −36, 58	12, −44, 58	−16, −46, 58	12, −48, 68
15	Cingulate sulcus			−14, −22, 42		−16, −24, 44	16, −28, 44
Premotor							
16	Precentral gyrus	−38, −2, 56	42, −4, 54	−38, −2, 54		−28, −6, 50	28, −8, 54
17	Posterior SFG			−22, −4, 68		−22, −4, 70	18, −6, 62

Figure 4. Comparison of the regions activated by observation of the 3 action classes at lower threshold. The red, green, and blue outlines plot the activation maps for climbing (CL), locomotion (LO), and manipulation (MA), respectively, at the $P < 0.01$ uncorrected level. The local maxima of the activation maps in parietal and premotor cortices are indicated in these same colors. Other conventions as in Figure 3.

manipulation activation is less extensive and more rostral compared with that for the other 2 classes. In the premotor cortex, climbing activation and to some degree also activation for observing locomotion extends more dorsally than the manipulation activation. Finally, in occipito-temporal cortex, the posterior MTG/STS activation is more extensive for the observation of manipulative actions than for the other 2 classes. Few differences between observing climbing and observing locomotion are discernible in Figure 4, although a comparison at the higher threshold (Fig. 3A,B) indicates that the levels of activation in SPL are clearly higher for observing climbing than for locomotion. In the subsequent sections, we will investigate which regions are more involved in observing 1 class than the other 2, but also the regions involved in observing all 3 classes of actions.

In Figure 4, the ventral shift for activations associated with observing manipulation compared with those for observing climbing is clearly discernible in both parietal and premotor cortex. This is consistent with the parallel parieto-frontal circuits described anatomically in the nonhuman primate (Rizzolatti and Luppino 2001). Yet, the shift toward ventral regions in the premotor cortex seems restricted compared with the activations reported by Jastorff et al. (2010). To compare the topographies of premotor activations in these 2 studies, we used the miniROIs defined by Jastorff et al. (2010), but extended them dorsally beyond the superior frontal sulcus to include the present activations, particularly those induced by observing climbing (Fig. 5). The peaks in the activations elicited by observing manipulation in the present study are indeed close to the maxima of the earlier study: miniROI 3 on the right and miniROI 7 on the left (Jastorff et al. 2010). Furthermore, the premotor activation for observing climbing was strongest in the most dorsal miniROIs, where the results of Jastorff et al. (2010) indicated that observations of foot and
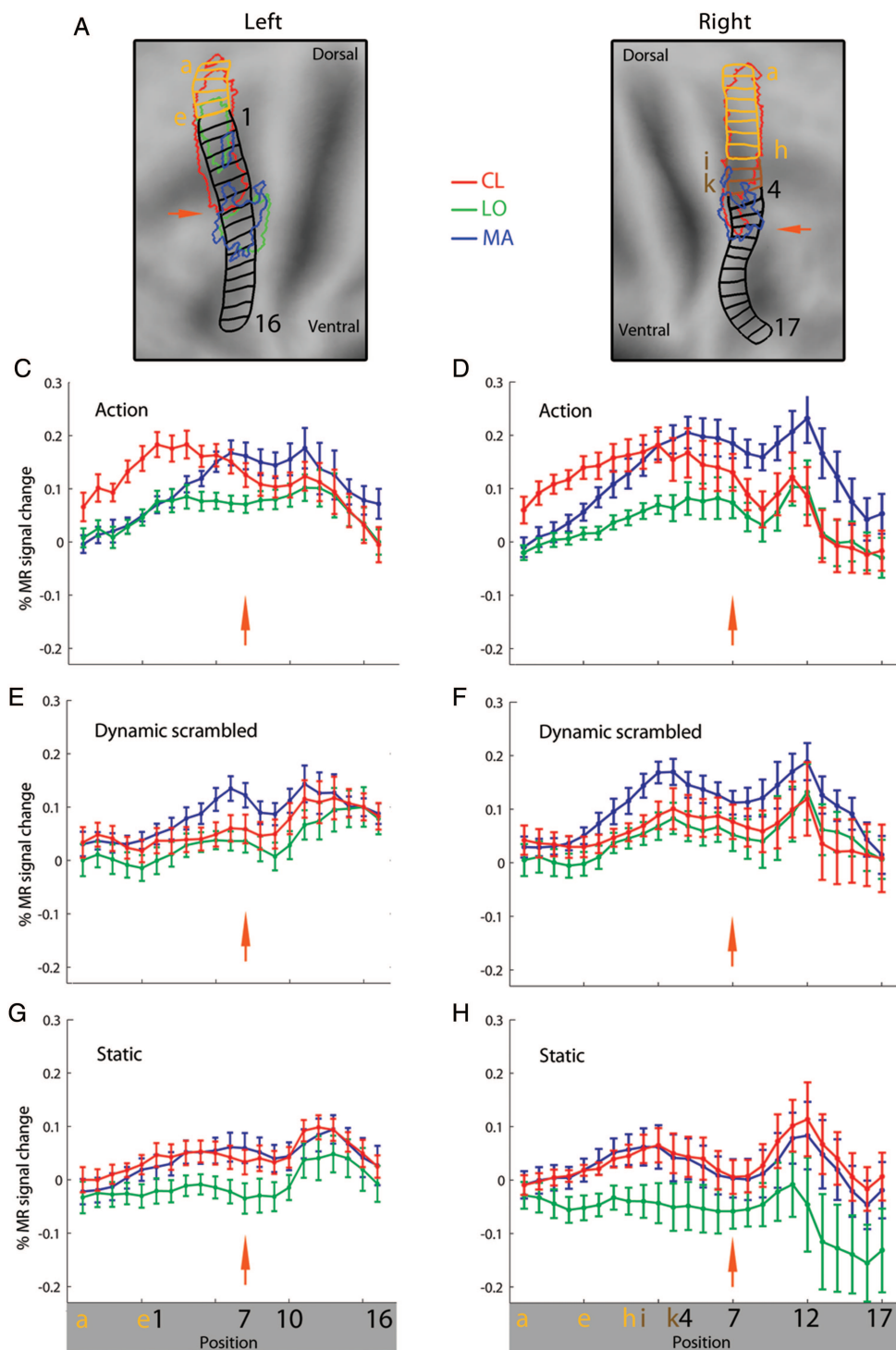
Figure 5. Activity profiles of premotor activation sites. (*A* and *B*) Outlines of miniROIs defined in the present study (designated with yellow letters *a* to *h* in RH, *a* to *e* in LH), taken from Jastorff et al. (2010), but modified for the present study (bronze, letters *i* to *k*) and defined in (Jastorff et al. 2010) (black, numbers) overlaid onto the flatmaps showing the left (*A*) and right (*B*) premotor components of the masks for the observation of the 3 action classes: climbing (red outlines), locomotion (green outlines), and manipulation (blue outlines); (*C* and *D*) mean (±standard error of the mean, SEM) MR activity in % signal change from fixation for the observation of the 3 action classes (same color as in *A* and *B*) plotted as a function of the miniROI position in left (*C*) and right (*D*) premotor cortices. (*E* and *F*) Mean (±SEM) MR activity in % signal change from fixation baseline for the dynamic scrambled controls of the 3 action classes (same colors as in *A* and *B*) plotted as a function of the miniROI position in left (*E*) and right (*F*) premotor cortices. (*G* and *H*) Mean (±SEM) MR activity in % signal change from fixation baseline for the static controls of the 3 action classes (same colors as in *A* and *B*) plotted as a function of the miniROI position in left (*G*) and right (*H*) premotor cortices. Red arrows: putative border between dorsal and ventral premotor cortex taken from Tomassini et al. (2007).

hand actions were represented. Interestingly, electrical stimulation of this cortical region in the monkey evokes climbing movements (Graziano et al. 2002).

Nevertheless, no activation pattern, even that for observing manipulative hand actions, extended beyond miniROIs 7 on the right or 10 on the left (blue outlines in Fig. 5A,B), located near the boundary between dorsal and ventral premotor cortex suggested by diffusion tensor imaging measurements of Tomassini et al. (2007, red arrow). Therefore, we plotted the MR signal change, with respect to fixation, for action observation as a function of the miniROI position in Figure 5C,D, in order to compare them with similar plots for the dynamic scrambled condition (Fig. 5E,F), the more stringent of the 2 controls (Fig. 2), and also for the other, static control (Fig. 5G,H). Clearly, observing manipulation, when compared with fixation, also activates more the ventral parts of the premotor cortex, reaching a peak at miniROIs 11 or 12. However, the dynamic scrambled control for manipulation activates the premotor cortex more strongly than the dynamic scrambled controls of the other actions and evokes activation levels almost equal to the experimental condition in the more ventral miniROIs. The strong premotor activation elicited by the dynamic scrambled control of manipulative actions may reflect our decision to keep the scrambling grid constant across videos, despite the relatively limited extent of motion in the manipulative action videos compared with locomotion or climbing videos. Indeed, activation patterns for the static conditions of climbing and manipulation are more similar. In conclusion, this analysis shows that even with respect to fixation, observation of climbing and manipulation clearly dominate within distinct regions of the premotor cortex, with the activation evoked by observing manipulation culminating more ventrally than the activation induced by observing climbing. In addition, the premotor activation elicited by observing climbing and locomotion differ most sharply in the dorsal sectors of the premotor cortex.

Regions Showing a Preference for Observation of One of the Action Classes: Action Class Interaction Maps

To demonstrate that a region is more concerned with the observation of one class of action than with the others, we tested the interaction between the factors class of action and type of video in a given direction. Next, we took the conjunction of the 2 interaction terms having a given class in the first part of their expression. This conjunction SPM thus defined the interaction for observing a given class of action. For example, to define interaction of observing climbing (Fig. 6A), we conjoined the interaction climbing greater than manipulation, relative to their controls, with the interaction climbing greater than locomotion, relative to their controls. This conjunction was then inclusively masked with the visual mask and the activation map for observing climbing, and exclusively masked with the 4 contrasts defining the activation maps for observing locomotion and manipulation. The interaction maps (Fig. 6) plot the voxels that are more concerned with observing 1 class of action than the remaining 2, with respect to their controls (see Materials and Methods) and that are not differentially activated by observing these latter 2 classes relative to their respective controls.

Figure 6A shows the interaction map of observing climbing: Most if not all of the specific voxels of the interaction

map of climbing are included in the activation map of observing climbing, considered at the $P < 0.01$ uncorrected level (black outlines in Fig. 6A). The regions specific for observing climbing were similar in the 2 hemispheres and included anterior dorsal SPL, extending from the dorsal part of the postcentral sulcus, and adjoining crown of the hemisphere, posterior cingulate sulcus, dorsal premotor cortex, as well as 2 lateral occipital sites and posterior fusiform cortex bilaterally plus more posterior dorsal SPL and parieto-occipital cortex mainly in the left hemisphere. The anterior dorsal SPL sites included 470 voxels in the left hemisphere and 568 voxels in the right one. The activity profiles of representative voxels (red stars in Fig. 6A) for these 2 regions are shown for illustrative purposes in Figure 7A,B. Given that the local maxima of the interaction were close to the exclusion boundary, we chose as representative voxel for the left site a voxel near the middle of the site with a t-score in the interaction SPM close to that of the local maximum (red star in Fig. 7A). For the right site, we took a secondary local maximum, removed from the exclusion boundary, as representative voxel (red star in Fig. 7A). Notice that for the SPM analysis, we used the average of the controls, which are treated separately in this figure, providing information about the robustness of the interactions.

Figure 6B plots the interaction map for the observation of manipulative actions. In 2 anterior parietal regions, 1 STS and 1 left premotor region, the relative activation for observing manipulation was significantly greater than that for observing climbing or locomotion, and activation for observing locomotion or climbing was very small. As a result, a number of voxels (red to yellow), lying within the activation map at $P < 0.01$ uncorrected (black outline in Fig. 6B), were specifically activated by observing manipulation. They included 53 left parietal voxels in the confidence ellipse of phAIP, with a few voxels more anterior, 89 voxels in right phAIP, 23 voxels in right STS, and also 41 ventral premotor voxels. It is noteworthy that the regions specific to climbing observation (Fig. 6A) clearly avoided the confidence ellipses of phAIP, dorsal IPS anterior, and DIPSM, which are believed to correspond respectively to anterior AIP, posterior AIP, and anterior LIP in the lateral bank of monkey IPS (Durand et al. 2009). In contrast, the regions specific for observing manipulation fell within phAIP bilaterally (Fig. 6B). The activity profile of a voxel representative for the right anterior IPS region (blue star in Fig. 6B) is shown in Figure 7C for the 2 control conditions separately, to illustrate the robustness of the interactions. The left anterior IPS activation site was strongly elongated in the direction of the upper bank of the IPS. Hence, it appeared small in the flatmap and, although it was 53 voxels large, no 27 voxel ROI could be fitted to this activation without including a large fraction of unspecific voxels.

The interaction map for locomotion was devoid of any results with regard to this analysis. Indeed, the interaction between observing locomotion and manipulation yielded several significant voxels in the direction of a stronger activation for observing locomotion. These were located in lateral occipital cortex, parieto-occipital cortex, anterior precuneus, and posterior cingulate sulcus bilaterally. However, not a single voxel was more differentially active, relative to controls, for observing locomotion compared with observing climbing. Thus, observing locomotion activates a subpart of the regions involved in the observation of climbing, as can also be seen in Figure 4.
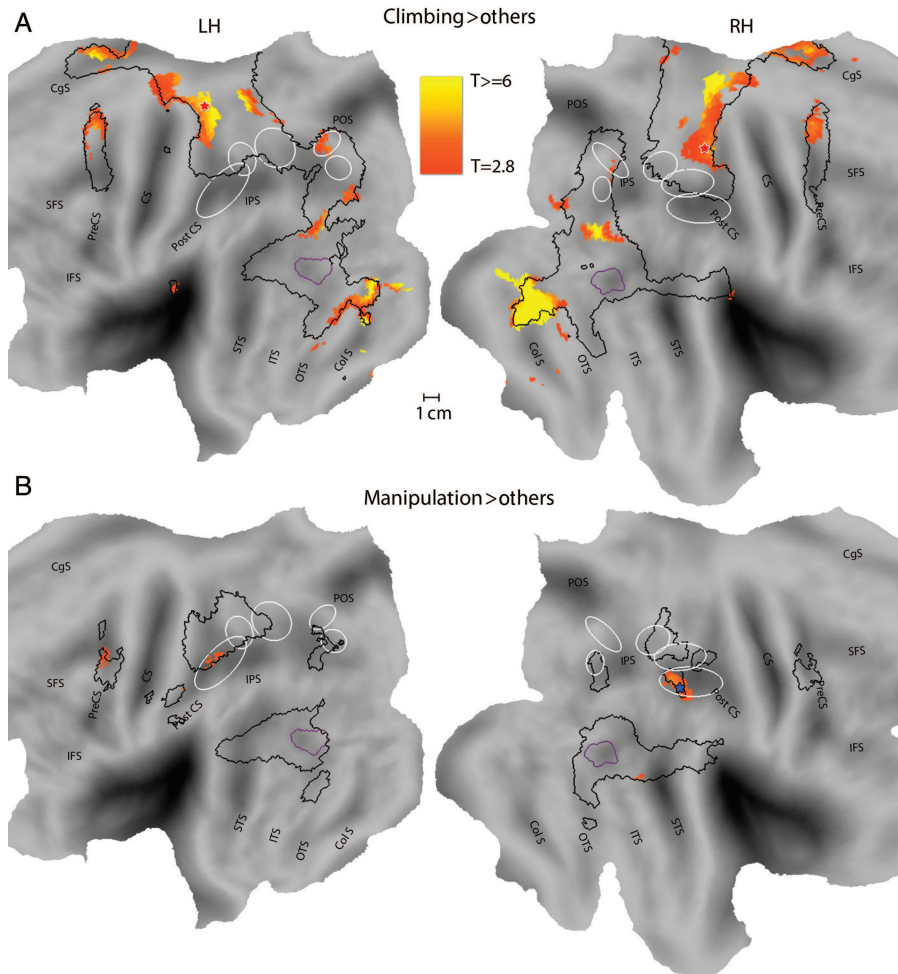
Figure 6. Interaction maps for the observation of climbing (A) and manipulation (B). Voxels (red to yellow) significant in the interactions comparing observation of climbing to observation of locomotion and manipulation (A) and observation of manipulation to observation of climbing and locomotion (B), inclusively masked with the map for observation of climbing (A) and manipulation (B) and with the visual mask, both at $P < 0.05$ uncorrected, and exclusively masked with the contrasts observation of locomotion minus static, observation of locomotion minus dynamic scrambled control, observation of manipulation minus static, observation of manipulation minus dynamic scrambled control (A) and with the contrasts observation of locomotion minus static, observation of locomotion minus dynamic scrambled control, observation of climbing minus static, observation of climbing minus dynamic scrambled control (B), all 4 taken at $P < 0.03$ uncorrected, projected onto the flatmaps of the 2 hemispheres. The color scale indicates the t-scores of the interaction maps (thresholded at $P < 0.05$ FDR corrected). Black outlines correspond to the activation maps for observation of climbing (A) and manipulation (B), at $P < 0.01$ uncorrected, corresponding to the outlines in Figure 3A,C. Red and blue stars indicate voxels on which the ROIs used in Figure 7 are centered; the red star in the right hemisphere indicates a secondary local maximum (see yellow voxels).

Regions Common to the Observation of all 3 Classes of Actions: The Common Action Activation Map

Figure 4 suggested that there was also overlap between the various regions activated by observing the 3 action classes. Figure 8 shows in brown the voxels that were significant in the conjunction of the 3 activation maps at $P < 0.05$ FDR corrected, the same level as used for the interaction maps in Figure 6A,B. Only 3 activation sites were common to the 3 action classes (Fig. 8): One site in left postcentral sulcus, dorsal of phAIP (70 voxels), and left and right posterior ITS sites (252 and 343 voxels, respectively). The left postcentral sulcus site had its local maximum at −32, −40, 60 (Table 2) with a secondary maximum at −32, −44, 72. The caudal parts of the pITS sites, in the posterior/lower bank, which included the local maximum, were located near hMT/V5+ taken from an earlier study (Jastorff and Orban 2009), and the extrastriate body area (EBA), as these 2 regions overlap considerably (Peelen et al. 2006; Jastorff and Orban 2009). In parietal cortex, it is

noteworthy that the common region in left postcentral sulcus (70 voxels) is similar in size to the 2 phAIP regions in the manipulation interaction maps (89 and 53 voxels), though the latter appeared smaller in the flatmap, because of the orientation of the region with respect to the outer surface of the hemisphere and deformations of the flatmap. When the threshold in the conjunction was lowered to $P < 0.01$ uncorrected for illustrative purposes (brown outlines in Fig. 8), several sites appeared in the right parietal cortex, notably in right DIPSM and a right postcentral sulcus site, symmetrical to the significant site in the left hemisphere. In addition, 2 parieto-occipital sites were activated at this level, the caudal part of which overlapped with the ventral intraparietal sulcus (VIPS) confidence ellipses in both hemispheres.

The common activation map (Fig. 8) was relatively restricted, perhaps surprisingly so, given the overlap seen in Figure 4. This common map was in fact the result of a conjunction of 6 contrasts, and it has been suggested that the
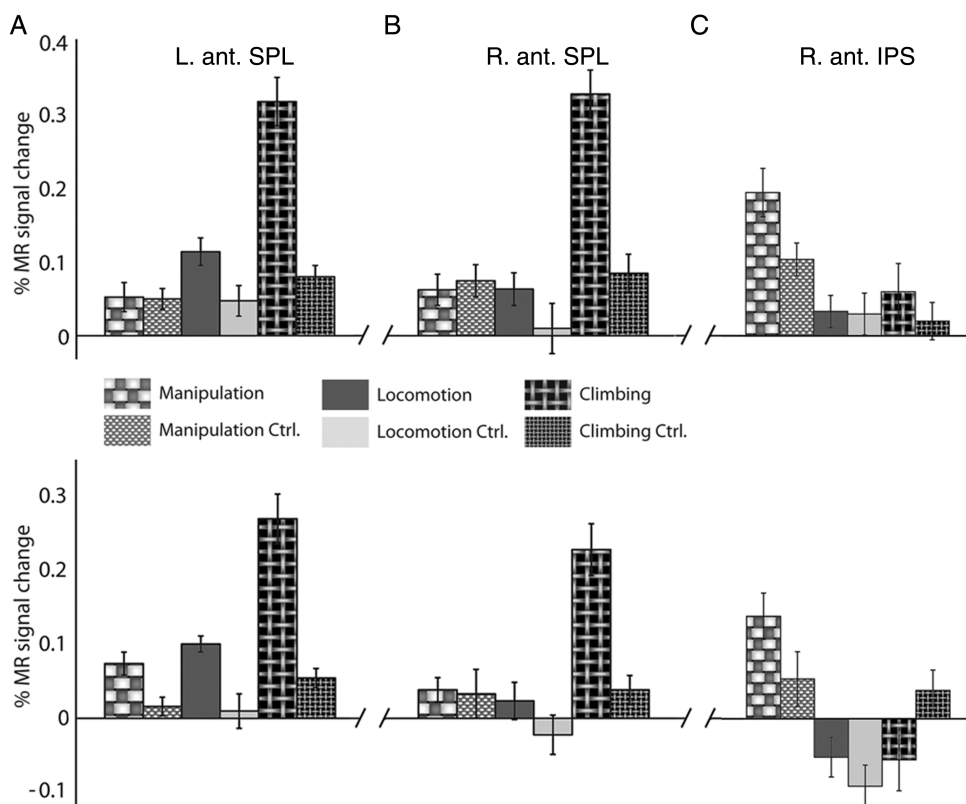
Figure 7. Activity profiles of parietal ROIs centered on representative voxels of the observation of climbing and observation of manipulation interaction maps. Activity profiles of left and right anterior SPL ROIs centered on −18, −46, 66 (A) and 24, −46, 72 (B) and of right anterior IPS ROI centered on 42, −46, 46 (C) are plotted separately for the runs with static controls (top row) and dynamic scrambled controls (bottom row). Conditions are indicated by pattern code in the inset, Ctrl. indicates the control condition. Vertical bars: SEM
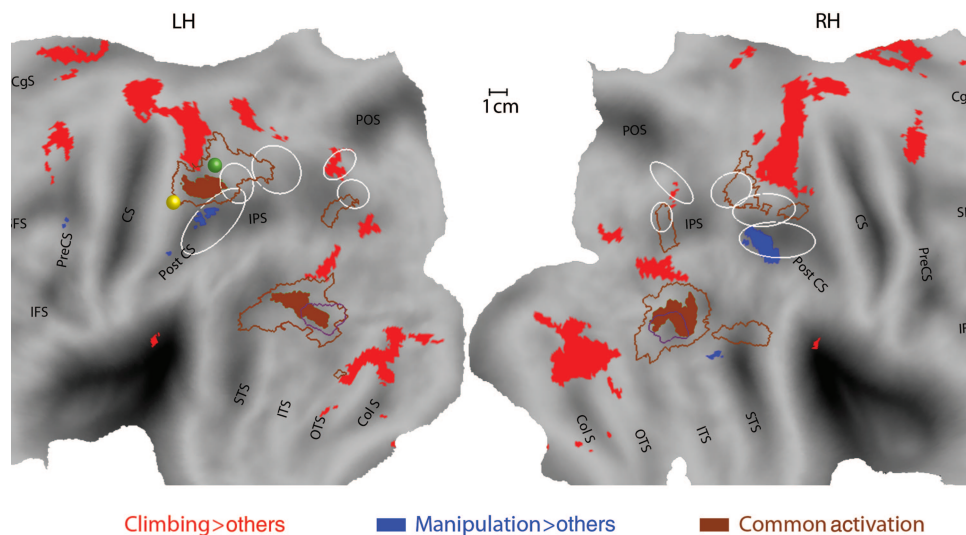

Figure 8. Common activation map for observing the 3 actions. Voxels significant in the conjunction of the 3 activation maps, at $P < 0.05$ FDR corrected (filled brown) and $P < 0.01$ uncorrected (brown outlines), compared with the interaction maps of climbing (red, same as Fig. 6A) and manipulation (blue same as Fig. 6B). Anterior IPS activation site from Ehrsson et al. (2005) (yellow dot, −45, −39, 60) and from Gentile et al. 2011 (green dot, −32, −46, 62); other conventions as in Figure 3.

number of significant voxels may decrease with the number of contrasts, when using the conjunction null (Friston et al. 2005). To confirm the result obtained in Figure 8, we also investigated the regions common to pairs of actions observation, requiring only 4 contrasts to be conjoined. Figure 9 plots these regions using the same format as that of Figure 8: The brown voxels are those mutually activated by a pair of actions yielded by conjunction, and the red, green, or blue voxels correspond to the voxels yielded by the interaction in either direction, thus differentially active in one class

Table 2.
Local maxima of activation sites common to observing classes of actions

Location	All 3 actions	Manipulation/locomotion	Manipulation/climbing	Climbing/locomotion
Occipito-temporal				
Left pITS	−50, −72, 6	−50, −72, 6	−50, −70, 6	−48, −76, 0
Right pITS	46, −74, −2	46, −74, −2	52, −68, 4	46, −76, −2
Right STS			56, −40, 16	58, −44, 14
Parietal				
Left postcentral sulcus (PVBR)	−32, −40, 60	−32, −40, 60	−32, −44, 72	−32, 40, 58
Right postcentral sulcus (PVBR)				32, −38, 56
Left DIPSM				−24, 60, 58
Right DIPSM				24, −54, 54
Left POIPS				−22, −86, 38
Right POIPS				16, −82, 40
Left VIPS				−30, −86, 26
Left CSv				−14, −20, 42
Left precuneus				−10, −42, 58
Right precuneus				14, −44, 54
Frontal				
Left dPM				−22, −6, 68
Left insula				−22, −28, 4
Right insula				18, −28, 6

VIPS, ventral intraparietal sulcus; dPM, dorsal premotor; PVBR, parietal visual body region.

compared with the other, relative to their controls. To remain consistent with the definition of the interaction maps in Figure 6, the interactions shown in Figure 9 were exclusively masked with the 2 contrasts defining the activation map of observing the control action class, both at $P < 0.03$ uncorrected. This analysis basically confirmed the results shown in Figure 8. The regions common to observing climbing and manipulation, as well as to observing locomotion and manipulation corresponded to 3 regions of the common activation map (Table 2) with the addition of a small site in the right STS for the pair climbing–manipulation. Only for the pair locomotion–climbing (Fig. 9C) were there many more regions activated in common, as predicted from the individual activation maps (Figs 3 and 4). However, these regions can now be subdivided into 3 groups: 1) a group of regions also common to the other pairs, and thus also to the common activation map for all 3 classes (left postcentral sulcus, pITS bilaterally), 2) a group common to all 3 classes but at a descriptive level of $P < 0.01$ (right postcentral sulcus, bilaterally DIPSM and VIPS), and 3) regions that are common only to the pair climbing–locomotion, in left cingulate sulcus, precuneus bilaterally, as well as a dorsal extension of the parieto-occipital site into the parieto-occipital intraparietal sulcus (POIPS) confidence ellipses bilaterally (Table 2).

Control Experiment
The aim of the control experiment was to test whether the differences between observing the 2 versions of locomotion (with and without background) had any effect on the comparison between observing different classes of actions. We were particularly concerned that the weaker activation in the locomotion activation map than in the climbing activation map might be confounded by differences in the respective backgrounds of these videos. To verify the consistency of the results in the control and the main experiment, we mapped the activations of observing climbing and locomotion (without background, as in the main experiment). These 2 maps (Supplementary Figure S1) were similar to those shown in Figure 3. Next, we directly compared the activation maps for the 2 versions of locomotion. This interaction analysis revealed a number of occipital regions that were significantly more

activated by observing locomotion$_{bg}$ than by observing locomotion without background, as used in the main experiment. However, these regions not only were relatively restricted (Fig. 10A), but they were located almost entirely outside the region significant in the observing climbing > observing locomotion interaction, the component of the climbing interaction map that could have been influenced by the difference in background conditions. Since we were interested in the relative balance of the activations for observing climbing and observing locomotion, no exclusive masking was applied in the analysis of the control experiment.

To verify that differences in the locomotion backgrounds indeed had little effect on our results, we directly compared the interactions observing climbing > observing locomotion and observing climbing > observing locomotion$_{bg}$ (Fig. 10B). These 2 maps were relatively similar in the parietal cortex, with most differences occurring in the lateral occipital and ventral occipital cortices. The similarity of these maps was further underscored by the proximity of their local maxima (Supplementary Table S1). Most local maxima of the interaction observing climbing > observing locomotion were also present in the interaction map observing climbing > observing locomotion$_{bg}$, with the exception of the posterior fusiform, posterior lingual, and parieto-occipital maxima. The activity profiles (Supplementary Fig S2) confirmed that the activation evoked by observing locomotion$_{bg}$ was generally similar to that elicited by observing locomotion, with 2 exceptions: It exceeded that evoked by locomotion observation modestly in parieto-occipital ROIs and more clearly in the posterior fusiform and lingual ROIs. Direct testing of the interaction background present/absent with the factor locomotion/control revealed significant interaction (after correction for 24 tests) for both types of runs only in the posterior lingual ROI of the right hemisphere: $F_{1,18} = 43.3$, $P < 10^{-4}$ for the dynamic scrambled runs and $F_{1,18} = 14.8$, $P < 0.0015$ for the static runs. In the posterior fusiform ROI of the left hemisphere, the interactions did not reach significance: $F_{1,18} = 4.5$, $P < 0.05$ for the dynamic scrambled runs and $F_{1,18} = 1.2$, $P < 0.3$ for the static runs. The activity in these ventral occipital ROIs was also increased to some extent for the control conditions of locomotion$_{bg}$, suggesting that their activity was related to the
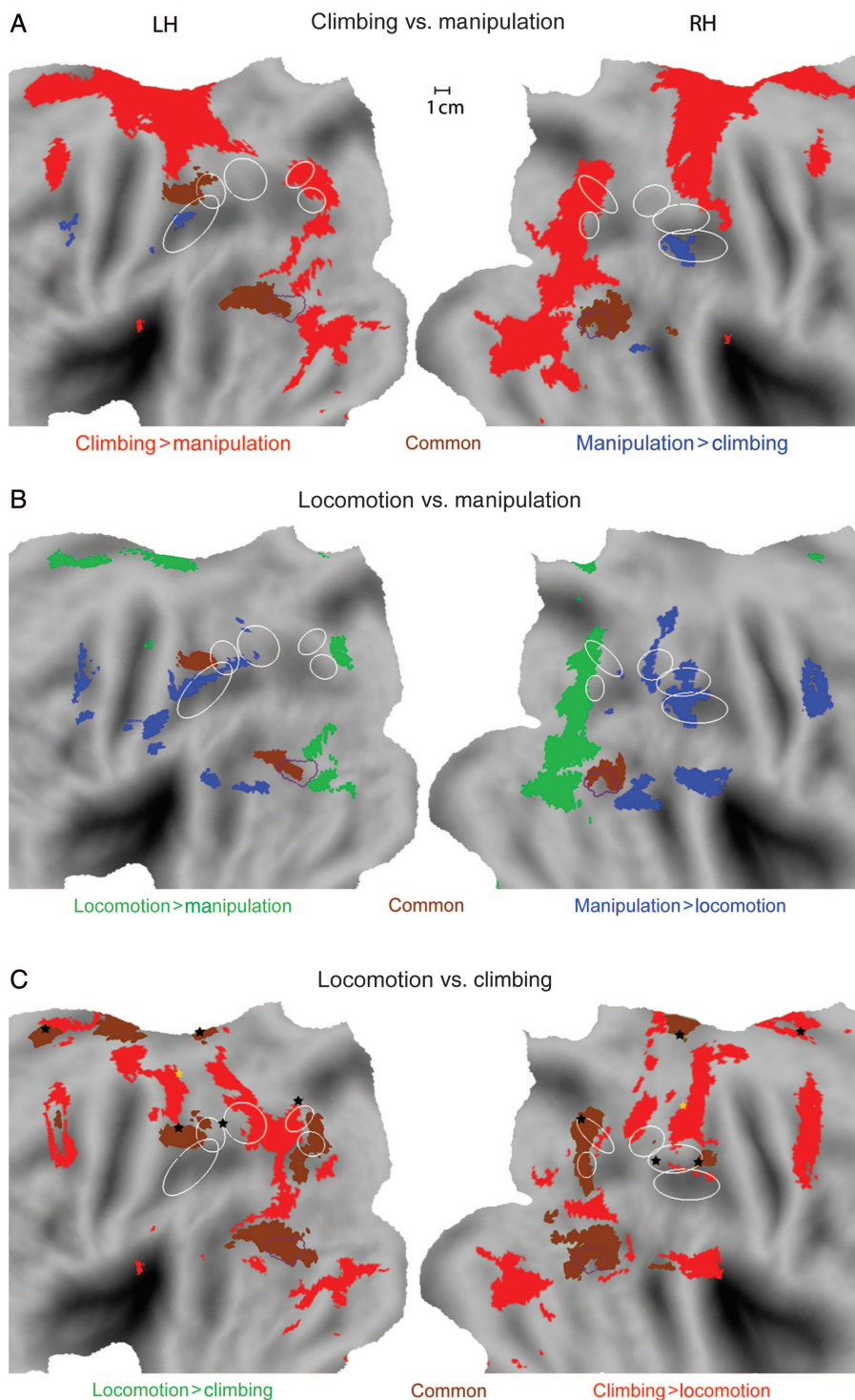
Figure 9. SPMs for interactions between and conjunction of pairs of action classes observation: Manipulation–climbing pair (*A*), manipulation–locomotion pair (*B*), and climbing–locomotion pair (*C*). Red voxels: Interactions climbing > manipulation, exclusively masked with the contrasts observation of manipulation versus static control and observation of manipulation versus dynamic scrambled control (both at $P < 0.03$ uncorrected) in *A* and climbing > locomotion, exclusively masked with the contrasts observation of locomotion versus static control and observation of locomotion versus dynamic scrambled control (both at $P < 0.03$ uncorrected) in *C*; blue voxels: Interaction manipulation > climbing, exclusively masked with the contrasts observation of climbing versus static control and observation of climbing versus dynamic scrambled control (both at $P < 0.03$ uncorrected) in *A*, manipulation > locomotion exclusively masked with the contrasts observation of locomotion versus static control and observation of locomotion versus dynamic scrambled control (both at $P < 0.03$ uncorrected) in *B*; and green voxels: locomotion > manipulation, exclusively masked with the contrasts observation of manipulation versus static control and observation of manipulation versus dynamic scrambled control (both at $P < 0.03$ uncorrected) in *B* and locomotion > climbing exclusively masked with the contrasts observation of climbing versus static control and observation of climbing versus dynamic scrambled control (both at $P < 0.03$ uncorrected) in *C* (but no voxel satisfied these criteria); brown voxels: Conjunction ($P < 0.05$ FDR corrected) between the 2 actions of the pair. Black stars in *C*: Optic flow activation sites from Cardin and Smith (2010): ventral intraparietal sulcus (CSv), precuneus; putative 2v (p2v); putative VIP (pVIP), ad putative V6 (pv6). (Orange stars: SPL activation sites from Bakker et al. (2008). Other conventions as in Figure 3.
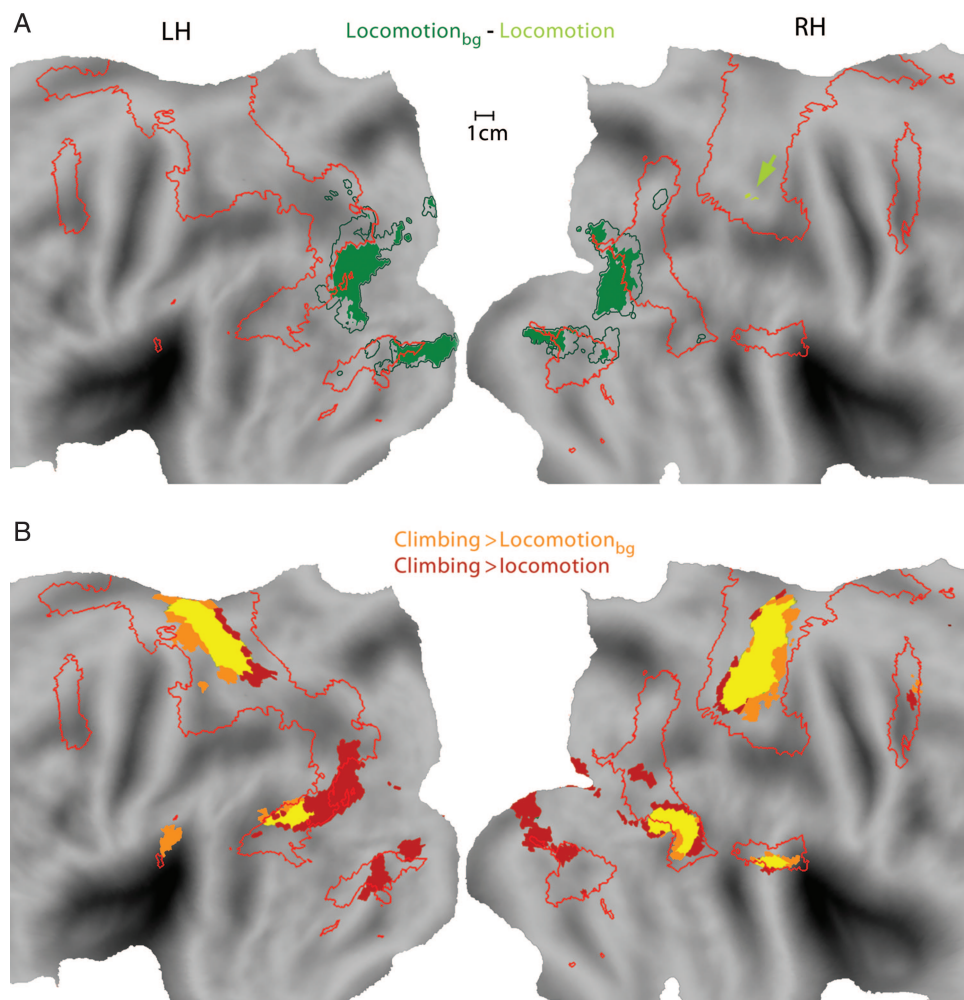
Figure 10. Control experiment. (*A*) Comparison of the activation maps for the 2 versions of locomotion: Voxels reaching significance $P < 0.05$ FDR corrected or $P < 0.01$ uncorrected in the interaction observing locomotion$_{bg}$ > observing locomotion plotted in dark- and light-green, respectively, and voxels reaching $P < 0.01$ uncorrected in the interaction observing locomotion > observing locomotion$_{bg}$ in yellow–green (indicated by arrow) on flattened left and right hemispheres. (*B*) Comparison of the interactions observing climbing > observing locomotion and observing climbing > observing locomotion$_{bg}$: Voxels reaching FDR significance in these interactions are indicated in dark red and orange, respectively, and their overlap in yellow. Red outlines in *A* and *B*: Limits of interaction observing climbing > observing locomotion from the main experiment.

processing of the textured background, as mentioned above (Fig. 2), and in agreement with results of Peuskens et al. (2004) and Cant and Goodale (2007). The extended analyses carried out upon the control experiment have confirmed that the removal of the background in most locomotion videos had little or no effect on our comparisons between observing the various action classes in the parietal cortex. In addition, the control experiment has replicated the results obtained in the main experiment, even if most subjects were common to both experiments.

Discussion

Our results show that large expanses of the PPC were activated by observing the actions of others, including both regions that were specifically involved in observing either climbing or manipulation and regions that were common to observing all 3 classes of actions.

Functional Organization of the Human Parietal Cortex Involved in Action Observation

Our results indicate that the observation of climbing recruits parietal regions which are distinct from those involved in observing manipulation or locomotion. Both left and right rostral parts of dorsal SPL satisfy the most stringent criteria for segregated processing based on interaction tests at corrected level and exclusive masking at low level with the activation for observing locomotion and observing manipulation, all relative to the 2 control conditions. Similarly, we also found that observing manipulation specifically recruits anterior IPS regions in the vicinity of phAIP. Although these regions were smaller, they satisfy the same stringent criteria. These phAIP activation sites were located near those reported by Jastorff et al. (2010) for the observation of positive and negative manipulative actions.

While the first 2 predictions derived from the functional hypothesis (organization according to the action class) were born out, the third prediction that observing locomotion

should involve parietal regions different from those engaged by the observation of manipulation and climbing has clearly failed to materialize. Even though several regions showed stronger activations for the observation of locomotion compared with manipulation, no such distinctions were obtained between the observations of locomotion and climbing. This can be taken as evidence favoring the effector hypothesis, since the component interaction that failed is one of those distinguishing between effector and class of action predictions. However, as stated in the Introduction, the component that fails compares 2 action classes, locomotion and climbing, that may have some functional similarities, in that they both have a common goal: Moving the body in space. This may mitigate the argument against the functional organization of the parietal cortex.

With 2 tests supporting the functional hypothesis (climbing interaction and manipulation interaction) and 1 test which is more or less ambiguous (locomotion interaction), the balance of the evidence indeed favors the hypothesis advanced by Jastorff et al. (2010) that some parietal areas involved in action observation are organized according to the class of action observed, not the effector. Comparison of any of the 3 pairs of action observation separately would also point toward a similar conclusion. Heed et al. (2011) investigated the parietal regions involved in planning hand, foot, and eye movements. While they obtained some degree of segregation between eye movement planning, activating the more posterior occipito-parietal regions, and limb movement planning, activating SPL, there was little segregation between planning of upper and lower limb movements, except anteriorly in area 5. Whereas, these experiments provided evidence against the effector-based organization, they did not provide evidence in favor of an action type organization. It should be noted, however, that the action executed with the hand and feet was of the same type: Reaching.

The videos used in the present study not only differed with respect to the class of actions portrayed and the effectors performing these actions, but also in the number of limbs involved in the actions. Indeed, manipulative actions involved a single limb, the right hand, while climbing involves all 4 limbs. Locomotion is typically performed by moving the lower limbs, but the upper limbs generally move in synchrony with the legs. Thus, an alternative explanation of our findings could theorize that parietal cortex is organized depending on whether actions observed involve a single limb or multiple limbs, or alternatively, unilateral or bilateral movements of the body. There is little evidence in the present experiment that allows us to simply dismiss the limb-number hypothesis, but a comparison with other studies make this hypothesis less attractive. Indeed observation of reaching actions, another typical single-limb action, involves very different parietal regions than those involved in observing manipulative actions (Jastorff et al. 2010, this study), according to Filimon et al. (2007). In a recent study, we (Heitger, Macé, Jastorff, Swinnen and Orban unpublished) compared the parietal regions involved in the observation of unimanual and bimanual manipulative actions and found that the same anterior IPS regions were involved in the observation of both types of manipulative actions, although the parietal activation was more symmetrical for the observation of the bimanual actions. This clearly suggests that the number of limbs used in the action does not influence, which parietal regions are engaged by action observation.

The number of limbs involved in the actions observed, however, may well explain the difference in size of the PPC regions devoted to observing climbing compared with those devoted to manipulation observation. The videos of these 2 classes of actions also differ in other visual aspects, such as the part of the visual field where the actions occur, or the background present in the videos. The influence of the latter factor, however, has been shown to be minimal by the control experiment. Given the differences in the extents of the action regions in the videos, modulation by spatial attention might contribute to the greater extent of the cortex devoted to observing climbing versus observing manipulation. This may account for the presence of dorsal occipital and fusiform regions among the climbing specific regions, most likely reflecting activity in peripheral parts of middle and far extrastriate areas, which are much more susceptible to attention modulation than V1 (Tootell et al. 1998).

PPC Regions Activated by all 3 Classes of Actions

Even though at low threshold ($P < 0.01$ uncorrected) there seems to be considerable overlap between the 3 classes of actions, the overlap was in fact relatively restricted for a threshold of $P < 0.001$ uncorrected when a conjunction of 6 contrasts was required. The latter threshold was identical to the one used to identify activations specific for only 1 action class. They included 1 parietal region in dorsal postcentral sulcus and 2 symmetrical occipito-temporal activation sites in the banks of posterior ITS. Interestingly, the caudal parts of the pITS sites overlap extensively with the motion sensitive region hMT/V5+, which itself overlap extensively with the EBA (Peelen et al. 2006; Jastorff and Orban 2009). Since the action videos always included the complete body of the actor, part of the common activation seen in pITS may reflect a higher order visual process different from action observation: The visual processing of changing human body shapes. The rostral part of the pITS sites extends beyond EBA and may really reflect the common visual processing, at least at the voxel level, of the various actions of conspecifics.

A similar explanation may also apply to the left postcentral sulcus region. There might however be an intriguing alternative explanation. The region lies very close to the region involved in the somatosensory body image (Ehrsson et al. 2005) and to the regions activated by both the vision and the touch of the subject's own hand (Gentile et al. 2011), indicated by colored dots in Figure 8. Thus, instead of subserving action observation, this parietal region may correspond to the second visual body area postulated by Urgesi et al. (2007), as being involved in maintaining a configural representation of the human body across all its actions, different from EBA which provides a local description of the human body (Taylor et al. 2007).

At a lower threshold ($P < 0.01$ uncorrected), other parietal regions also common to the observation of the 3 action classes became apparent, notably DIPSM and VIPS. These regions have been shown to be involved in the processing of 3D structure from motion (3D SFM). Indeed, DIPSM and VIPS were defined as motion sensitive regions (Sunaert et al. 1999) that were also shown to be involved in 3D SFM (Orban et al. 1999). As argued by Orban (2011), the human body has a very complex 3D shape and body movements should therefore drive 3D SFM processing regions well. That the DIPSM

and VIPS regions were less involved in the observation of manipulation than in observing the 2 other classes may simply reflect the smaller size of the action regions in the manipulation videos. This size effect should be strongest for POIPS, another 3D SFM region (Orban et al. 1999), which has been shown to represent peripheral vision more than central vision (Orban et al. 2006), possibly explaining why it did not reach even $P < 0.01$ uncorrected in the conjunction of the 3 action classes, while it did so in the conjunction climbing–locomotion.

Further studies, however, are needed to investigate whether the commonly activated parietal regions form a substrate common to the observation of actions in general, or reflect higher order visual processes or cognitive processes other than action observation: Maintaining the configuration of the body across all its shape changes and extracting depth structure from the moving retinal input.

SPL and Precuneus Activation by Action Observation and Planning

Our results show that the observation of actions activates most, if not all, of human SPL, including its extension onto the medial wall. This result agrees with the recent study of Filimon et al. (2007). These authors studied the execution, mental visualization, and observation of reaching movements, using viewing the static targets of the reaching action as a control. Compared with this control, the observation of reaching activated the dorsal SPL region, extending into the precuneus, but entailed a more posterior part of SPL than that involved in climbing observation in the present study. The activation of several SPL regions by the observation of dancing video sequences has been reported by Calvo-Merino et al (2006). Dorsal SPL and neighboring precuneus and IPS regions have been implicated in the planning of limb movements by several studies (Astafiev et al. 2003; Connolly et al. 2003; Medendorp et al. 2005; Beurze et al. 2007; Hinkley et al. 2009; Cavina-Pratesi et al. 2010; Gallivan et al. 2011; Heed et al. 2011). Together with our results, these studies suggest that the same parietal regions involved in planning, and thus executing, actions are also engaged by observing these actions, as has been directly demonstrated by Filimon et al. (2007) for reaching actions and by Dinstein et al. (2007) for grasping.

Of course, it would be impossible, given the current technology, to compare the execution and observation of climbing in an MR scanner. Direct support for the hypothesis that the same parietal regions are involved in both observing and planning a given class of actions is thus difficult to obtain for climbing. There are, however, several lines of indirect evidence supporting this view, relying on similarities among the cortical regions involved in the planning of climbing and locomotion, both of which propel the subject through the environment and which use, to a certain degree, similar sensory information, such as optic flow or postural information. These planning regions may not overlap completely, since subjects use mainly their feet to move over a surface during bipedal locomotion, while climbing engages all 4 limbs for moving in 3 dimensions. Furthermore, climbing may require more complex visual information at a relatively close range, while bipedal locomotion has evolved to cover much wider distances, for which senses other than vision

may be important. Thus, one would expect that the planning of climbing involves both specific regions and regions common to locomotion and climbing, just as we found for the observation of climbing.

If we accept that some cortical regions are involved in the planning of both locomotion and climbing, indirect support for the matching hypothesis can be derived from optic-flow studies, since the planning of climbing and locomotion must to some degree depend on the extraction of heading from optic flow. Initial studies of heading discrimination implicated DIPSM (Peuskens et al. 2001). The regions involved in the processing of visual cues for self-motion have been mapped recently by Cardin and Smith (2010), who compared egomotion-consistent and -inconsistent flow. One would expect, under the matching hypothesis, to find overlap between those regions (black stars in Fig. 9C) and those that we found to be involved in climbing and locomotion observation. Figure 9C indicates that the match is excellent for VIPS (−10, −23, 39 and 11, −25, 40), which corresponds to our posterior cingulate sulcus activation sites (−14, −26, 40 and 16, −28, 44) and also for the optic flow precuneus sites (−14, −46, 48 and 11, −49, 47) which are close to the precuneus sites common to observing locomotion and observing climbing (−10, −42, 58 and 14, −44, 54). The p2v sites for optic flow are close to the common postcentral sulcus region in both hemispheres. On the other hand, their putative V6 and putative VIP show no overlap with our common locomotion and climbing regions. It may be that pV6 (Pitzalis et al. 2010) and also pVIP are indeed involved in extracting optic flow, but less so in using optic flow to control locomotion or climbing. Indeed, the matching hypothesis (see above) would then predict no activation of pV6 and pVIP by observing locomotion or climbing.

If we accept that some cortical regions are involved in the planning of both locomotion and climbing, the experiments studying the mental visualization of locomotion also become relevant. Indeed, we can compare them with the sites common to observing locomotion and observing climbing, which were located mainly in the medial wall, in anterior precuneus, and posterior cingulate sulcus. Imagery of locomotion tasks has been tested in a positron emission tomography study (Malouin et al. 2003). Comparing the imagining of standing, initiating gait, walking, or walking with obstacles (all in first-person perspective) with being at rest, systematically yielded activations of the precuneus and dorsal premotor cortex bilaterally. Furthermore, imagining walking with or without the presence of obstacles yielded bilateral activation of the precuneus (−17, −59, 54 and 12, −64, 65), about 10 mm posterior to our precuneus sites (see above). A subsequent MR study confirmed the involvement of dorsal SPL (−16, −50, 64 and 16, −54, 64) and dorsal premotor cortex in imagery of normal and precision gait (Bakker et al. 2008). These latter sites (orange stars in Fig 9C) were located just posterior the boundary of the dorsal SPL sites specific for climbing, indicating that they belonged to the interaction map observing climbing > observing locomotion, but were excluded because of weak activation (t-score between those of $P < 0.05$ corrected and $P < 0.03$ uncorrected) by observing locomotion.

Our results also suggest that part of the precuneus may serve a function that is much more action related than is apparent from human imaging studies, most of which have implicated the precuneus in self-centered mental imagery

strategies and episodic memory retrieval (for review Cavanna and Trimble 2006). The present results indicate the need for caution in the interpretation of imaging results concerning precuneus, as motor functions related to whole-body actions cannot be studied directly in the MR scanner (see above). However, bimanual coordination can be investigated and has been found to activate anterior precuneus and dorsal premotor cortex (Wenderoth et al. 2005). Bimanual coordination is a key component of the planning and execution of climbing actions; hence, it is fitting that bimanual motor coordination activates regions likely to be involved in the planning of climbing. Our results showing an activation of the anterior precuneus by the observation of climbing are also in agreement with the recent connectivity study of Margulies et al. (2009). These authors describe an anterior sector of the human and monkey precuneus that is extensively connected with dorsal and medial motor cortices and dorsal SPL. It is likely that one of the functions of such a network is the planning and execution of climbing actions. The precuneus is not only activated when subjects view optic flow (see above), it is also active when subjects experience linear self-motion arising from optic flow (Wolbers et al. 2008). However, the regions involved in updating information about surrounding objects during self-motion engage more ventrally located precuneal regions than those we found involved in observing climbing.

Further support for the precuneus and dorsal SPL playing roles in the control of locomotion and climbing comes from electrical cortical stimulation experiments and from the ictal features of a patient with epilepsy caused by a lesion of the right paramedian precuneus. The sensations of body rocking or tilting experienced by this patient suggest that the precuneus processes static otholitic information (Wiest et al. 2004). Finally, bilateral damage to these dorsal parietal regions can cause egocentric disorientation (Kase et al. 1977; Aguirre and D'Esposito 1999; Wilson et al. 2005) with intact recognition of landmarks or familiar places.

Theoretical Views on PPC Function

Even if one could provide incontrovertible evidence that the same PPC regions are activated by both the execution and the observation of various actions, this only suggests, but does not prove, that they may house neurons resembling the mirror neurons that have previously been described in the monkey for grasping (Fogassi et al. 2005; Rozzi et al. 2008). This hypothesis, which would explain why mirror like neurons may underlie action understanding in general and not just that of grasping, is difficult to address in humans using fMRI. Recently, however, Mukamel et al. (2010) recorded neurons in human medial frontal regions that were selective for the execution of grasping or facial gestures and for observing those same actions. Unfortunately, these neurons were not more numerous than those in which selectivity for execution and observation did not match, and the proportions of either type differed little from those of similar neurons recorded in the medial temporal cortex. Our results suggest that it would be more fruitful to study locomotion or climbing in medial wall neurons, but again this may be technically difficult, at least with regard to the motor execution aspect. Thus, further work is needed to confirm our basic premises that the functional organization of the PPC according to the type of

actions applies to action observation because 1) regions involved in planning and observation match (although many more neurons may be involved in panning than in observation) and 2) the PPC regions involved in action planning are organized according to the type of action.

The organization according to the type of action is one of the 3 dimensions according to which the frontal motor regions are organized (Graziano and Aflalo 2007). It may well be the case that a similar dimension-reduction scheme is applicable to parietal cortex, retaining 2 of the dimensions used for the frontal cortex: Type of action, for which the present study provides support, and region of the space targeted by the action, but replacing the third dimension, the actions involving similar muscles, with actions using sensory information about similar aspects of the outside world (3D space, 3D objects or human bodies).

Comparison with Monkey

It is very likely that the dorsal SPL region involved in observing climbing includes the human homolog of area PEc in the monkey. Several lines of indirect evidence indicate that area PEc might be involved in the motor control of locomotion or climbing. Many neurons of this region are selective for optic flow (Raffi et al. 2002) with selective influences arising from both the focus of expansion and the position of the eyes (Raffi et al. 2010). Many neurons also are somatosensory in nature and are selective for joint positions of the upper limb and, less frequently, the lower limb (Breveglieri et al. 2008). Area PEc projects to dorsal premotor cortex (F2) (Matelli et al. 1998; Marconi et al. 2001; Bakola et al. 2010) and receives afferents from area V6A (Gamberini et al. 2009). Thus, V6A is in a position to relay visual motion information to both MIP, which is involved in the visual control of reaching (Andersen and Cui 2009), and PEc. These neurophysiological and anatomical data are in line with our results, which in turn suggest that PEc may control climbing as much as it does locomotion (Breveglieri et al. 2006, 2008; Bakola et al. 2010). This hypothesis provides an explanation as to why V6A neurons are not only reaching selective (Fattori et al. 2001) but are also grasping selective (Fattori et al. 2010): They contribute to the visual control of grasping in order to climb, rather than to manipulate or to feed. In the same vein, it may be that the reach and oculomotor neurons that have been reported in PEc (Ferraina et al. 2001) contribute a different behavioral function (to climb) than those observed in MIP or LIP (to point to, touch or grasp objects; Andersen and Cui 2009).

The parietal regions specifically involved in observing grasping and manipulation include parts of phAIP, in agreement with the putative homology of this region with monkey AIP (Durand et al. 2009), an area known to control hand actions (Fogassi et al. 2001), to respond during grasping execution (Nelissen et al. 2011), and also to action observation (Nelissen et al. 2011). The parietal regions activated by observing manipulation in the present study extended further caudally to include regions likely to be involved in the more general function of extracting 3D SFM. The activation of a more restricted set of parietal areas in the monkey, chiefly AIP and PFG, by observing grasping is consistent with the reduced 3D SFM activation in the parietal cortex of monkeys compared with humans (Vanduffel et al. 2002). In general, it is possible that the various functional domains within human SPL

involved in the planning and observing of different classes of actions correspond to the parietal functional territories delimitated in the monkey by electrical stimulation: Grasping involving rostral and ventral regions, reaching somewhat more dorsal regions, and climbing even more dorsal regions (Kaas et al. 2011). While further experiments are needed to relate monkey and human findings, our results show that the observation of widely different classes of actions, such as manipulation and climbing, activates different regions of human PPC, together with regions that are activated in common.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/

Notes

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